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Effects of stand age on soil respiration in *Pinus massoniana* plantations in the hilly red soil region of Southern China

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ABSTRACT

It is of great importance to assess the effect of stand age on soil respiration (SR) to understand the potential carbon sequestration capacity of afforestation. In this study, we investigated the changes in SR and microclimate variables in a chronosequence of four different aged stands (8-, 17-, 27-, and 36-year-old) in a *Pinus massoniana* plantation in the soil erosion area of southern China. SR was found to have obvious seasonal dynamics among the four aged stands, and the highest and lowest value in summer and winter, respectively. We also found that SR increased with increasing stand age, and the mean SRs for the 8-, 17-, 27-, and 36-year-old stands were 1.45, 1.83, 2.03, and 2.32 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$, respectively. Furthermore, all stands showed that SR increased exponentially with increasing soil temperature and that the temperature sensitivity of SR (Q_{10}) was 2.08, 2.09, 2.23, and 2.19 for 8-, 17-, 27-, and 36-year-old stands, respectively. Moreover, the Q_{10} values for the 27- and 36-year-old stands were significantly higher than those of the other two stands ($p < 0.05$). Stepwise multiple regression analysis indicated that soil temperature had a greater effect on SR than soil organic carbon. This study provides insights for estimating SR in *P. massoniana* plantations in the eroded area of southern China and highlights the need to consider the effect of stand age and seasonal patterns when predicting the carbon budget under different future climate change scenarios.

1. Introduction

Soil respiration (SR) is a major carbon flux in global carbon cycling and is defined as the release of CO_2 from the soil via the plant roots, soil microbes, and fauna (Hanson et al., 2000; Wang et al., 2013; Lai et al., 2017; Z. Zhao et al., 2017). Globally, SR reaches 66–100 Pg C y^{-1} from terrestrial ecosystems (Raich and Schlesinger, 1992; Jian et al., 2018), which is second only to gross primary productivity (100–120 Pg C y^{-1}), and higher than the estimated net primary productivity (50–60 Pg C y^{-1}) (Field et al., 1998). Even a subtle change in SR may cause a large fluctuation in atmospheric CO_2 concentration, and consequently influence the global carbon cycle (Schlesinger and Andrews, 2000; Pregitzer and Euskirchen, 2004; Fa et al., 2018). Furthermore, a number of recent studies have reported that the estimated global annual SR has remarkably increased by 0.04–0.1 Pg C y^{-1} over the past few decades (Bond-Lamberty and Thomson, 2010; Hashimoto et al., 2015; Z. Zhao et al., 2017), and therefore, presents an important positive feedback for global warming and may ultimately affect human survival. Thus, a better understanding of SR and the mechanisms that determine changes in it are of great importance in estimating the status of carbon emissions in terrestrial ecosystems and estimating the carbon balance, and subsequently contributes to understand the missing carbon sink issues in the regional and global carbon cycle (Raich et al., 2002; Xiao et al., 2009; Han et al., 2017; Cunha et al., 2018).

Forests cover ~4.0 billion ha of the global land area (FAO, 2016) and constitute a major reservoir of global soil carbon (Xu and Qi, 2001; Gough et al., 2005). Based on the difference between photosynthesis and respiration, forest ecosystems can act as a carbon source or a carbon sink (Saiz et al., 2006), and thus many scientists have studied the mechanisms of changes in SR changes and the driving factors. However, most previous studies have focused on the relationship between SR and climatic variables, such as temperature and precipitation (Wang et al., 2004; Yan et al., 2010; Zhou et al., 2013), and only a few studies have assessed the effects of the structure parameter of forests, particularly stand age, which can determine the distribution of ecosystem carbon pools (Wang et al., 2013). To date, the effect of stand age on SR remains unclear. As the stand age increases, SR can (1) increase due to increasing root biomass, microbial biomass, and substrate

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Table 1
Properties of four different aged *Pinus massoniana* forest stands measured in Fujian Province, China.

Stand (age)	H (m)	DBH (cm)	Tree density (stem ha^{-1})	LAI ($m^2 m^{-2}$)	CC (%)	Slope (°)	Understory species
PM8	4.07(1.07)	4.43(0.92)	1300(198)	1.76 (0.29)	42 (4)	10	Dicranopteris dichotoma Berhn.
PM17	5.68(1.15)	7.19(2.14)	1975(282)	2.57 (0.20)	67 (6)	7	*D. dichotoma* Berhn.
PM27	8.20(1.20)	8.22(2.56)	1525(438)	2.90 (0.26)	79 (9)	8	D. dichotoma Berhn., *Lespedeza bicolor* Turcz.
PM36	9.05(1.95)	9.52(3.23)	1425(409)	2.91 (0.42)	82 (11)	5	D. dichotoma Berhn., *Setaria viridis* (L.) Beauv., *L. bicolor* Turcz.

PM8, PM17, PM27, and PM36 represent 8-, 17-, 27-, and 36-year-old *P. massoniana* stands, respectively. H, DBH, LAI, and CC represent tree height, diameter at breast height (1.3 m), leaf area index, and canopy cover, respectively. Data are shown as means and standard errors in parentheses.

availability (Wiseman and Seiler, 2004; Xiao et al., 2014); (2) decrease due to decreased and fine root biomass (Saiz et al., 2006; Yan et al., 2011; Zhao et al., 2016a); or (3) show no obvious linear relationship to stand age because of the combined effects of various factors (Wang et al., 2011; Y. Ma et al., 2014; Powers et al., 2018). These findings are inconclusive, and it is still unclear as to how SR changes with stand age.

Although the global forest area has declined over the past two decades, the planted forest area has increased, and had reached 291 million ha in 2015 (FAO, 2016). Despite producing important commercial products, afforestation can be used to reduce greenhouse gas emissions, control soil erosion, and increase terrestrial carbon sequestration (Reay et al., 2007; Zhao et al., 2016b), and has been considered to be a mutually beneficial strategy (Yan et al., 2011). The use of afforestation is of great importance for the restoration of the ecological environment in the hilly red soil region of southern China, especially in the soil erosion area. Masson pine (*Pinus massoniana* Lamb.), one of the most important tree types in southern China, has been widely planted in this ecologically and environmentally vulnerable area because of its high adaptability to drought and barren soils and its capacity to retain water and nutrients (Tian et al., 2010; Z. Ma et al., 2014). *Pinus massoniana* plantations cover about 10 million ha and which accounts for approximately 20% of the planted forests in southern China (Yang et al., 2011; SFA, 2014). An improved understanding of the relationship between planting *P. massoniana* and increasing carbon flux would assist future afforestation management. Therefore, there has been an increased research focus on *P. massoniana* in carbon sequestration and carbon cycling studies (Chen et al., 2013; Justine et al., 2015). However, studies on the link between SR and stand age in *P. massoniana* plantations are limited in southern China (Xiao et al., 2014).

Microclimate (temperature and soil water content) have been considered as the dominant factors of SR in most forest ecosystems (Vose and Bolstad, 2007; Huang et al., 2018). The exponential relationship between SR and soil temperature has been widely accepted (Saiz et al., 2006; Tu et al., 2013). A number of studies reported that the variation in SR is also regulated by canopy cover, leaf area index, root biomass, soil organic carbon, and soil total nitrogen (McCarthy and Brown, 2006; Bahn et al., 2008; Zhao et al., 2016a; Hursh et al., 2017). These factors are also used to determine the temperature sensitivity of SR (often expressed as Q_{10}), which is considered to be a possible feedback mechanism between the climate system and the carbon cycle in terrestrial ecosystems (Wang et al., 2016). Moreover, the Q_{10} value can vary with the stand age. Therefore, it is necessary to explore how stand age influences Q_{10} to further elucidate the influence of afforestation on regional or global carbon balance.

This study aims to improve the understanding of the effect of stand age on SR in *P. massoniana* plantations, in the soil erosion area of southern China. The SR of four different aged *P. massoniana* forest stands (8-, 17-, 27-, and 36-year-old) were assessed in each season from April 2017 to April 2018. The objectives of this study were to determine (1) the seasonal dynamics of SR and its correlated factors under different aged stands; (2) how SR changes with stand age; and (3) the main driving factors and their contribution to controlling the variations in SR.

2. Materials and methods

2.1. Site characteristics

The study sites were located in Hetian Town (25°33′–25°48′N, 116°18′–116°31′E), in Fujian Province, China. The area is characterized by a typical subtropical monsoon climate with a mean annual precipitation, mean annual temperature, and mean frost-free period of 1621 mm (occurs mainly from April to June), 19 °C, and 260 d, respectively (Liu et al., 2016; Wu et al., 2016). The soils are dominated by Ultisols (locally called “red soil”), which accounts for > 70% of the soils in the total study area. The average elevation is ~310 m above sea level (Gu et al., 2011). All study plots were dominated by *P. massoniana* plantations that had been established on former soil eroded land. In addition to the dominant species, other tree species in the plots included *Schima superba*, *Liquidambar formosana*, and *Lespedeza bicolor*.

2.2. Experimental design

To assess the effects of stand age on soil respiration, we selected four stand age classes, namely, 8-, 17-, 27-, and 36-year-old *P. massoniana* stands (hereafter called PM8, PM17, PM27, and PM36, respectively). There was > 4 ha of stand area in each age class of the *P. massoniana* forest stands. Stand age data were offered by the local forestry department. In each age stand, 20 m × 20 m plots were replicated three times, i.e., a total of 12 plots were established. More detailed information of the four stands of different ages are shown in Table 1. The tree density, canopy cover, and height and diameter at breast height (1.3 m) of trees in the sample plots were measured at the same time (McCarthy and Brown, 2006). To avoid differences in climate and soil type, and to ensure that differences in soil respiration were attributed to the different stand age classes, the distance between any two stands was < 10 km.

2.3. Measurements of soil respiration, soil temperature, and soil water content

SR was measured during a single sampling session that was conducted in each season from April 2017 to April 2018 (i.e., April 2017, spring; August 2017, summer; October 2017, fall; January 2018, winter; April 2018, spring) using a Li-8100 soil CO_2 flux system (LI-COR Inc., Lincoln, NE, USA). Within the 20 m × 20 m plots, three polyvinyl chloride (PVC) collars (20 cm inside diameter, 11 cm height) were randomly installed and inserted 4 cm into the soil before the first measurement. In order to avoid the effects of aboveground plants on SR, living plants inside the collars were clipped at the soil surface using scissors one day before each SR measurement. All SR measurements were taken between 09:00 and 16:00 to minimize the daily variation in SR. The mean SR for each PVC collar was determined from three replicates per measurement. The mean SR in each plot was calculated as the average values from the three collar measurements. The mean SR for each stand was determined from three replicated plots.

During SR measurements, soil temperature (ST) and volumetric soil water content (SWC) were recorded simultaneously. ST at 5 cm soil depth

and SWC were measured and automatically recorded using a LI-COR 8100 temperature probe (8100-201) and a LI-COR 8100 moisture probe (8100-204), respectively, that were inserted into the soil adjacent to each collar.

2.4. Measurements of leaf area index

The leaf area index (LAI) of study plots was collected using an indirect method, i.e., with the LAI-2200 plant canopy analyzer (LI-COR, Inc., Lincoln, NE, USA). All measurements were made at sunset or on cloudy days. Three LAI values were obtained for each plot using the remote mode of LAI-2200. We acquired an 'above-canopy' reading (A-reading) in the open areas near to the plots and four 'below-canopy' readings (B-readings) in the plot during each LAI measurement cycle (Behera et al., 2015). The LAI values were determined from the A- and B-readings. All B-readings were conducted at 180° view cap at 1.5 m from the ground level. The mean LAI value in each plot was calculated from three measured cycles. A total of 36 LAI values were measured in August 2017, January 2018, and April 2018.

2.5. Soil sampling and analysis

Soil samples were sampled from three depth intervals (0–20 cm, 20–40 cm, 40–60 cm) within each plot in August 2017, January 2018, and April 2018. For each plot, soils were sampled from three random pits and were combined to form a single composite sample. In total, 108 soil samples (i.e., 3 plots at 3 different depths in 4 different stands in 3 field soil sampling times) were transported to the laboratory for analysis. Prior to laboratory analysis, all rocks, leaf litter, and visible roots were removed. All soil samples were air dried and passed through 0.15 mm and 2 mm sieves to determine soil properties. Soil organic carbon (SOC) was measured using the $K_2Cr_2O_7$–H_2SO_4 wet oxidation approach (Tang et al., 2017), and total nitrogen (TN) was determined with a CN elemental analyzer (Vario Max, Elementar, Hanau, Germany). Carbon-nitrogen ratio (C/N) was determined using the ratio of SOC and TN. Soil pH was determined using a mixed soil suspension (soil:water, 1:3) and a glass electrode (Y. Ma et al., 2014).

2.6. Relationships between soil respiration and related factors

A classic parametric exponential function, using ST as the drive variable, has been widely used to determine the relationships between SR and ST (Saiz et al., 2006; Wang et al., 2013; Zhao et al., 2016a; J. Zhao et al., 2017). The function was calculated using the following equation:

$$R = ae^{bT} \quad (1)$$

where R is the measured soil respiration rate (μmol CO_2 m^{-2} s^{-1}), T is the measured soil temperature at 5 cm depth (°C), and a and b are fitted parameters that were acquired using a least squares nonlinear regression. The a value represents the basal respiration at temperature of 0 °C. The b value was used to determine the Q_{10} value using:

$$Q_{10} = e^{10b} \quad (2)$$

where Q_{10} is a temperature sensitivity index of SR, which was defined as the ratio between SR at a temperature of 10 °C higher than the given temperature (T + 10) to the SR at a given temperature (T).

In order to remove the effect of ST on SR, we calculated SR at 20 °C (R_{20}) according to Eq. (3) and then analyzed the correlation between R_{20} and SWC.

$$R_{20} = Re^{b(20-T)} \quad (3)$$

where R_{20} is soil respiration rate at a given temperature of 20 °C, other parameters (R, b, and T) are described in Eq. (1).

2.7. Statistical analysis

Data sets were tested for distribution normality using Shapiro-Wilk test. One-way repeated measures analysis of variance (ANOVA) was performed to compare SR, SWC, and ST in different aged stands. The effect of stand age on the SR, SWC, and ST was conducted using Duncan's post-hoc test. The same statistical step was used to compare SOC, TN, C/N, and pH at each soil depth (0–20 cm, 20–40 cm, 40–60 cm, and 0–60 cm) between different aged stands. Pearson correlation analysis was used to analyze the relationship between SR and environmental variables. Based on the correlation analysis results, a stepwise multiple regression analysis was performed to determine the possible effects of environmental variables on SR. All statistical analyses and plotting were performed using SPSS version 21.0 (SPSS Inc., Chicago, IL, USA) and OriginPro version 9.0 (OriginLab Corp., Northampton, MA, USA). All significant differences for the statistical analysis were taken at $p < 0.05$.

3. Results

3.1. Seasonal changes in soil respiration, soil temperature, and soil water content in the four aged stands

The seasonal patterns of SR in the four aged *P. massoniana* stands from April 2017 to April 2018, all showed pronounced single-peak trends, with a maximum SR value in summer and a minimum SR value in winter, irrespective of stand age (Fig. 1a). Such seasonal changes in SR were strongly correlated with variations in ST rather than the variations in SWC in all four aged stands. For example, ST first increased from spring to summer, and then decreased until winter in all aged stands (Fig. 1b), which was in accordance with the variations in SR. In contrast, SWC initially decreased sharply from spring to summer, and then increased until the next spring in all aged stands (Fig. 1c). The SR ranges of PM8, PM17, PM27, and PM36 were 0.42–2.97 μmol CO_2 m^{-2} s^{-1}, 0.79–3.88 μmol CO_2 m^{-2} s^{-1}, 0.87–4.84 μmol CO_2 m^{-2} s^{-1}, and 1.04–4.21 μmol CO_2 m^{-2} s^{-1}, respectively. SWC ranged from a low value of 12.73 ± 2.48% in summer 2017, to a high value of 31.42 ± 3.97% in spring 2017. PM8 had the highest average ST and PM36 had the highest average SWC during the study period (Table 2).

Further analyses displayed that the SR of PM36 in spring was significantly different from that of the other three aged stands ($p < 0.05$). However, we did not find significant effect of stand age on SR for fall. There was no significant effect of stand age on ST in PM17, PM27, and PM36. In addition, there was no significant effect of stand age on SWC (Table 2). In general, SR increased as stand age increased, and was the highest in PM36 and lowest in PM8. Although the highest value of ST for PM17, PM27, and PM36 was comparable (Fig. 1b), peak value of SR for PM17 (2.96 ± 0.47 μmol CO_2 m^{-2} s^{-1}) and PM27 (3.5 ± 0.54 μmol CO_2 m^{-2} s^{-1}) were 81.10% and 95.89% of that for PM36 (3.65 ± 0.47 μmol CO_2 m^{-2} s^{-1}). The peak value of SR for PM8 was 2.21 ± 0.53 μmol CO_2 m^{-2} s^{-1}, which accounted for only 60.55% of that for PM36.

3.2. Soil organic carbon, soil total nitrogen, soil carbon-nitrogen ratio, and soil pH at the four age stands

Fig. 2 displays the statistical comparison of SOC, TN, C/N, and pH between four different aged stands at four soil depths. SOC was found to decrease with an increase in soil depth (Fig. 2a). The SOC of PM36 was significantly higher than that of PM8 and PM17 at 0–20 cm, 40–60 cm, and 0–60 cm soil depth, but there was no significant difference from that of PM27. TN was also found to decrease with an increase in soil depth (Fig. 2b). PM8 had the lowest TN for each soil depth ($p < 0.05$). PM36 had the highest TN at 0–20 cm ($p < 0.05$), followed by PM27, PM17, and PM8; however, there was no significant difference from that of PM27 and PM17 for the depth of 40–60 cm.

As shown in Fig. 2c, there was no significant trend for C/N across soil depths and stand ages. PM8 had the highest C/N at 0–20 cm, 40–60 cm and 0–60 cm, while the highest value at the depths of 20–40 cm occurred in PM17. In contrast to the trends seen in SOC and TN, pH increased with soil depth, except for PM17 (Fig. 2d). The soil pH

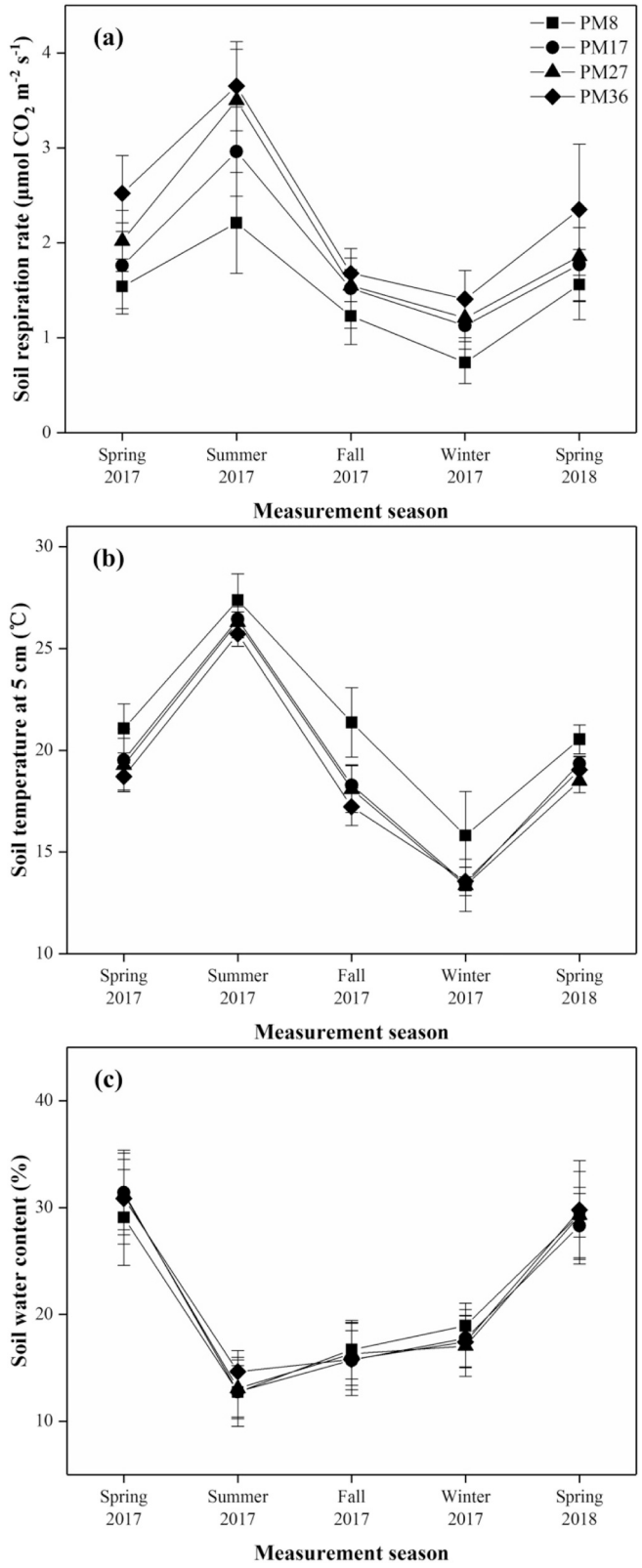

Fig. 1. Seasonal variations of (a) soil respiration rate, (b) soil temperature at 5 cm depth, and (c) soil water content for different aged *Pinus massoniana* forest stands in Fujian Province, China. Error bars indicate standard error. PM8, PM17, PM27, and PM36 represent 8-, 17-, 27-, and 36-year-old stands, respectively.

was the highest in PM8 for each soil depth ($p < 0.05$), whereas the soil pH of PM36 and PM27 was significantly lower than that of PM17 and PM8 at 0–20 cm.

3.3. Relationships between SR and the ST and SWC in different aged stands

SR increased with an increase in ST, according to the exponential function, with R^2 ranging from 0.60 to 0.84 (Fig. 3a). The soil basal respiration (a value) was the lowest in PM8, and significantly lower than that of the other aged stands ($p < 0.05$, Table 3). Furthermore, we found that the Q_{10} in PM27 and PM36 was significantly higher than that in the other two age stands ($p < 0.05$), i.e., the Q_{10} values were 2.08 in the PM8, 2.09 in the PM17, and 2.19 in the PM36, which were, respectively, 93.27%, 93.2%, and 98.21% of the corresponding Q_{10} value in the PM27 (Table 3). Unlike ST, no significant relationships between SWC and SR were found ($p > 0.05$), irrespective of stand age; furthermore, SWC could only explain 1–20% of R_{20} based on linear models (Fig. 3b).

3.4. Factors related to soil respiration

As shown in Table 4, SR was significantly correlated with LAI, ST, SOC, TN, C/N, and pH ($p < 0.05$), but was not significantly correlated with SWC ($p > 0.05$). Additionally, SOC was significantly correlated with other environmental variables (except for ST and SWC). We performed a stepwise multiple regression analysis to clarify the linear relationship between SR and the correlated variables (i.e., LAI, ST, SOC, TN, C/N, and pH), and the regression was standardized by zero-mean normalization to compare the relative importance of variables in Eq. (4). The model used was as follows, and the standardized regression coefficients are shown in the parenthesis:

$$SR = 0.136ST + 0.212SOC - 2.133\ (R^2 = 0.809, p < 0.01; ST: 0.747, SOC: 0.446) \quad (4)$$

The determination coefficient of this model was 0.81. The standardized regression coefficient of ST and SOC was 0.75 and 0.45, respectively, which indicated that ST had a greater effect on SR than SOC.

4. Discussion

4.1. The effect of stand age on soil respiration

The chronosequence method, in which time is replaced with different age stands, has been widely used in forest studies (Zhang et al., 2011; McElligott et al., 2016; Selvaraj et al., 2017). However, to date, few studies have assessed the effect of stand age on SR in pine forests (Irvine and Law, 2002; Powers et al., 2018). The results of the present study indicated that SR increases with stand age in *P. massoniana* forests, irrespective of season. This increasing trend has also been reported in the same tree species in the Three Gorges Reservoir Area, China (Xiao et al., 2014). In contrast, a decreasing trend in SR with stand maturation was found in *Pinus tabulaeformis* and *Populus davidiana* plantations (Zhao et al., 2016a). Y. Ma et al. (2014) found no significant effect of stand age on SR in a *Larix principis-rupprechtii* plantation. These results indicate that the response of SR to stand age differ with tree species, probably associated with the quality of soil C pools and amount of root biomass (Xiao et al., 2014). Although the PM36 site had the largest SR, the annual mean SR in this site was lower than that in the Three Gorges Reservoir Area (Xiao et al., 2014). This may be attributed to different edaphic conditions; for instance, our study area was characterized by serious soil erosion, leading to lower SOC and TN than those in the previous study, which probably limited microbial activities and reduced net primary productivity (Tu et al., 2013).

In general, the recovery phase of forest ecosystem will primarily shape litter and roots input patterns on a spatiotemporal scale, thus shifting SR by altering their substrate availability (Perez-Quezada et al., 2012; Wang et al., 2018). Due to the serious soil erosion before afforestation, the Masson pine plantations cannot change the poor soil condition in the early stage of recovery, and thus cannot provide substrate availability to SR. As *P. massoniana* forests progressively increase in size, canopy cover will also recover, likely increasing SOC and

Table 2
Seasonal changes in soil respiration (SR), soil temperature (ST), soil water content (SWC) in four different aged *Pinus massoniana* forest stands in Fujian Province, China.

	Season	PM8	PM17	PM27	PM36
SR (μmol CO_2 m^{-2} s^{-1})	Spring 2017	1.54(0.29)c	1.76(0.45)bc	2.02(0.32)b	2.52(0.40)a
	Summer 2017	2.21(0.53)c	2.96(0.47)b	3.5(0.54)a	3.65(0.47)a
	Fall 2017	1.23(0.30)a	1.52(0.42) a	1.55(0.17) a	1.68(0.16) a
	Winter 2017	0.74(0.22)c	1.13(0.25)b	1.21(0.21)ab	1.41(0.30)a
	Spring 2018	1.56(0.37)c	1.77(0.39)b	1.86(0.46)b	2.35(0.69)a
	All seasons*	1.45(0.59)c	1.83(0.73)b	2.03(0.87)ab	2.32(0.92)a
ST (°C)	Spring 2017	21.07(1.21)a	19.52(1.54)b	19.27(1.31)b	18.71(0.66)b
	Summer 2017	27.38(1.29)a	26.44(0.35)b	26.29(0.77)b	25.72(0.62)b
	Fall 2017	21.37(1.70)a	18.29(1.00)b	18.09(1.15)b	17.22(0.92)b
	Winter 2017	15.81(2.16)a	13.44(0.34)b	13.36(1.28)b	13.56(0.70)b
	Spring 2018	20.54(0.71)a	19.34(0.37)b	18.49(0.58)bc	19.03(0.65)c
	All seasons	21.24(3.99)a	19.41(4.28)b	19.10(4.31)b	18.85(4.05)b
SWC (%)	Spring 2017	29.28(4.48)a	31.42(3.97)a	31.22(3.30)a	30.86(4.26)a
	Summer 2017	12.73(2.48)a	12.76(3.23)a	13.07(2.69)a	14.64(1.99)a
	Fall 2017	16.71(2.73)a	15.72(2.78)a	16.33(2.95)a	15.80(3.39)a
	Winter 2017	18.94(2.12)a	17.78(2.68)a	17.06(2.85)a	17.43(2.43)a
	Spring 2018	29.36(4.03)a	28.31(3.59)a	29.29(2.04)a	29.78(4.62)a
	All seasons	21.36(7.48)a	21.19(8.04)a	21.39(7.93)a	21.74(7.89)a

PM8, PM17, PM27, and PM36 represent 8-, 17-, 27-, and 36-year-old stands, respectively. * indicates a statistical analysis of all measured data for each factor (SR, ST, and SWC). Different lowercase letters (a, b, and c) within each category indicate significant differences between age stands (one-way analysis of variance, Duncan's post-hoc test). Data are shown as means and standard errors in parentheses.

generating higher root growth, in turn increasing SR. The positive correlation between stand age and LAI, and SOC and TN reported in Table 1 and Fig. 2a and b, support the notion that the substrate availability and root biomass increase results in an increase in SR with stand development. Previous studies showed that vegetation litter provides the principal carbon source for microorganisms (Reichstein et al., 2003), which increases the microbial respiration (heterotrophic respiration). Moreover, a considerable proportion of SR (10%–90%) directly results from the vegetation via root or rhizosphere respiration (autotrophic respiration) (Hanson et al., 2000). Similar to what was reported by Lovelock (2008), we found that SR was significantly positively correlated with LAI (Table 4), which could reflect a wide

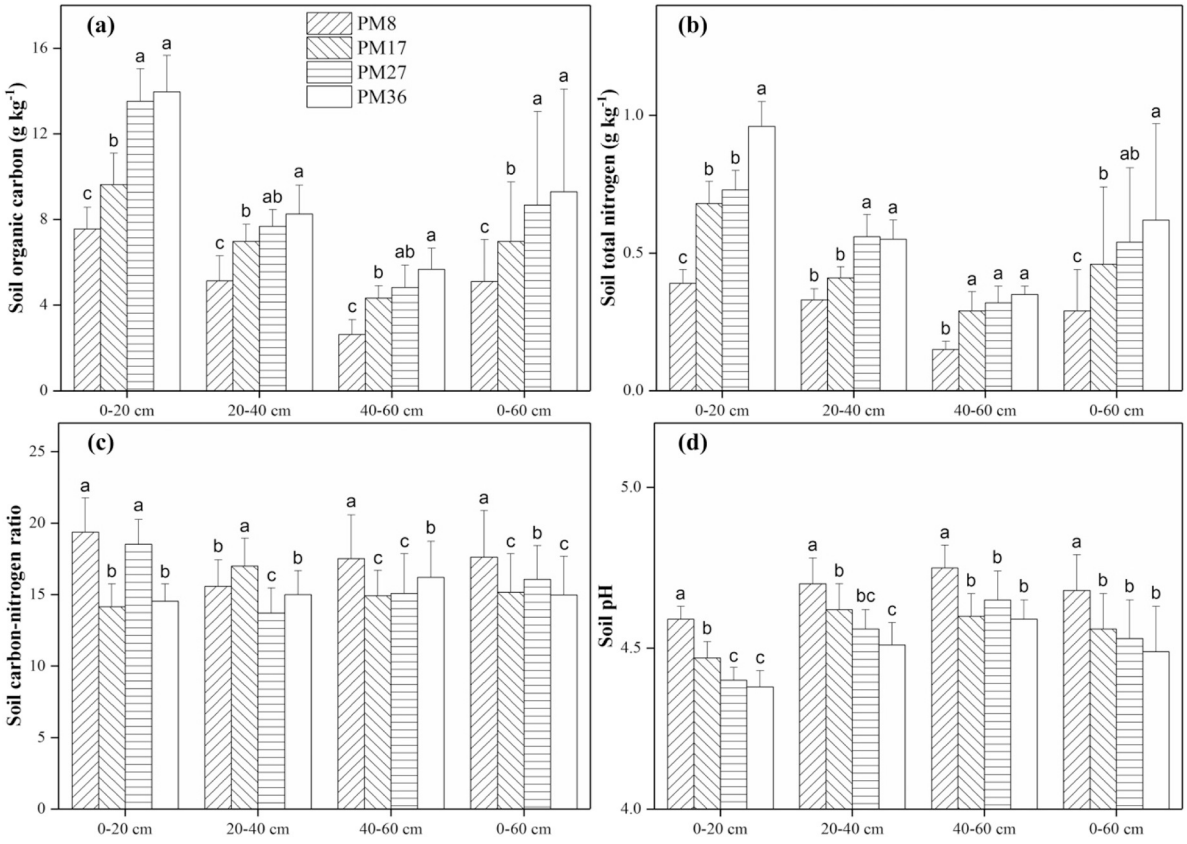

Fig. 2. Comparisons of (a) soil organic carbon, (b) soil total nitrogen, (c) soil carbon-nitrogen ratio, and (d) soil pH at four soil depths (0–20 cm, 20–40 cm, 40–60 cm, and 0–60 cm) in different aged *Pinus massoniana* forest stands in Fujian Province, China. Different lowercase letters (a, b, c, and d) within the same depth indicate significant differences between different aged stands (one-way analysis of variance, Duncan's post-hoc test). Error bars denote standard errors. PM8, PM17, PM27, and PM36 represent 8-, 17-, 27-, and 36-year-old stands, respectively.

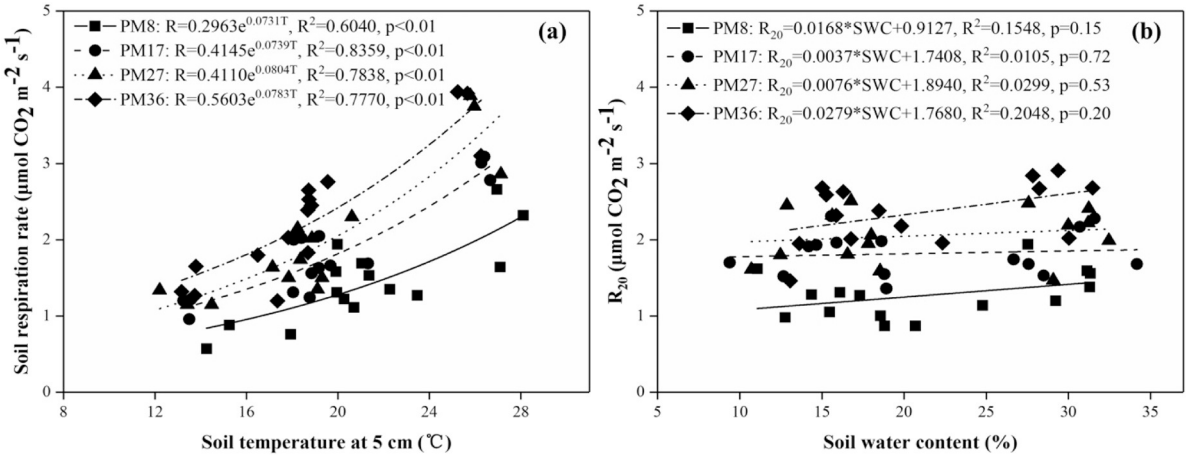

Fig. 3. The relationships between soil respiration (R_{20} (soil respiration at 20 °C)) and (a) soil temperature at 5 cm and (b) soil water content of different aged *Pinus massoniana* forest stands in Fujian Province, China. Plotted data points each represent the mean of nine measurements. PM8, PM17, PM27, and PM36 represent 8-, 17-, 27-, and 36-year-old of stands, respectively.

Table 3
Parameters and statistics of soil respiration model for each age stand based on Eqs. (1) and (2). *a* and *b* are the regression coefficients of Eq. (1). Q_{10} was calculated using Eq. (2). PM8, PM17, PM27, and PM36 represent 8-, 17-, 27-, and 36-year-old stands of *Pinus massoniana,* respectively, in the Fujian Province, China.

	a	b	R^2	p	Q_{10}
PM8	0.2963b	0.0731	0.6040	< 0.01	2.08b
PM17	0.4145a	0.0739	0.8359	< 0.01	2.09b
PM27	0.4110a	0.0804	0.7838	< 0.01	2.23a
PM36	0.5603a	0.0783	0.7770	< 0.01	2.19a

Different lowercase letters within the same column indicate significant differences between different age stands (one-way analysis of variance, Duncan's post-hoc test).

Table 4
Correlation analyses (Pearson correlation coefficients) between soil respiration (SR) and environmental variables in *Pinus massoniana* forest stands in the Fujian Province, China.

	SR	LAI	ST	SWC	SOC	TN	C/N	pH
SR	1	0.412*	0.782**	0.229	0.504**	0.387*	0.333*	−0.360*
LAI		1	−0.180	0.381*	0.744**	0.813**	0.107	−0.727**
ST			1	−0.065	0.078	−0.122	0.363*	0.081
SWC				1	0.298	0.402*	−0.036	−0.333*
SOC					1	0.855**	0.520**	−0.879**
TN						1	0.018	−0.812**
C/N							1	−0.388*
pH								1

LAI, ST, SWC, SOC, TN, C/N, and pH represent leaf area index, soil temperature, soil water content, soil organic carbon, soil total nitrogen, the carbon-nitrogen ratio, and soil pH, respectively. The sample size is 36.

* Indicate a significant difference at *p*-value of 0.05.

** Indicate a significant difference at *p*-value of 0.01.

variation in allocation to fine roots and litter. As an important structural parameter of the forest, LAI is often closely correlated to microbial biomass (Bolat and Öztürk, 2016) or root biomass (Cattanio, 2017). Although we did not directly measure root biomass and litter, the largest LAI was observed in PM36, which could be an indication of higher SR in PM36.

Soil respiration was significantly and positively correlated with SOC ($p < 0.01$) and TN ($p < 0.05$) (Table 4), which is in agreement with previous studies (Vose and Bolstad, 2007; Liang et al., 2015; Wang et al., 2016) that showed SR was affected by carbon and nitrogen substrate availability. This is because a higher SOC and TN can provide more energy for microbial activities and improve net primary productivity, and thus, an increase in SOC and TN could be indicative of an increase in microbial biomass and detrital substrate, both of which could lead to higher heterotrophic respiration of total SR (Wiseman and Seiler, 2004; Tu et al., 2013). Although afforestation with regular fertilization in the study region increased the input of nutrients, the low initial SOC and TN of severely eroded forestland, lead to a lower magnitude of SOC and TN (Fig. 2a and b); moreover, SOC and TN could constantly accumulate with continuing restoration (Li et al., 2018). Therefore, SOC and TN could increase with the restoration of forest ecosystem in the eroded hilly area, which may have increased the substrate supply for SR, thus leading to a higher SR.

4.2. Effects of soil temperature and soil water content on soil respiration under different stand ages

ST has been considered to be an important factor to explain the differences in SR in different aged stands (Yan et al., 2011; J. Zhao et al., 2017). Based on our results, it is clear that the ST in PM8 was significantly higher than that in other aged stands among the different seasons because of its lower canopy cover (Tables 1 and 2). Several studies have indicated that canopy cover is positively correlated with root respiration and SR (Reichstein et al., 2003), and can significantly affect ST (McCarthy and Brown, 2006). The lower canopy cover in PM8 may have increased ST by directly increasing the solar radiation on the soil surface (Tanaka and Hashimoto, 2006; Y. Ma et al., 2014). Consistent with the results reported from other studies (Chen et al., 2010; Zhao et al., 2016a; Powers et al., 2018), we observed a positive exponential relationship between SR and ST in our study (Fig. 3a), and thus, SR was higher in summer than in other seasons (Fig. 1a), irrespective of stand age. In the present study, ST could explain 60%–84% of SR variation for each age stand (Fig. 3a). Additionally, we observed that PM36 had abundant understory vegetation, the largest canopy cover, and the lowest ST in comparison with the other aged stands, which may have increased the root respiration and facilitated microbial activities by increasing litter production and the exudation of C-rich substances (Wang et al., 2011; Lei et al., 2017; Urrutia-Jalabert et al., 2017). In the present study, we did not measure the autotrophic and heterotrophic respiration, but the assessed factors (i.e., understory vegetation diversity, canopy cover, and ST) can partly explain the differences in SR among the different aged stands.

Some studies did not indicate a clear relationship between SR and SWC (Wang et al., 2013; Xiao et al., 2014; Powers et al., 2018), however, other studies showed a significantly positive relationship between SR and SWC (Zhao et al., 2016b; J. Zhao et al., 2017). In the present

study, no obvious relationship between SR and SWC was found, indicating that SWC was not a major driver of SR variation in our study. This may be attributed to the abundant precipitation in our study area and the high capacity of *P. massoniana* forests to retain water, leading to sufficient SWC (Tian et al., 2010). Raich and Potter (1995) reported that SWC is a major driver of SR only when soils are extremely dry or extremely wet. Therefore, it is possible that the 13%–30% range in SWC in our system did not limit microbial activities and root respiration.

The Q_{10} value has often been used to describe the sensitivity of SR to soil temperature (Wang et al., 2008; Zhao et al., 2016b). According to Raich and Schlesinger (1992), the value of Q_{10} ranged from 1.3 to 3.3 among various ecosystems. In this study, the Q_{10} values varied from 2.08 to 2.23 in the different age stands of *P. massoniana*, which are consistent with the results reported by previous studies in subtropical forests (Sheng et al., 2010; Tu et al., 2013; Huang et al., 2018) and lower than the value reported in a *Populus davidiana* forest (Zhao et al., 2016a). One or more of the following reasons could explain this phenomenon. First, the phenological activity of deciduous plants is more significant than that of coniferous species because of increased root activity in spring, leading to higher Q_{10} values (Yuste et al., 2004). Second, higher Q_{10} values tend to occur under conditions of high substrate availability rather than under conditions of low substrate availability (Gershenson et al., 2009; López-Serrano et al., 2016). Due to long-term soil erosion, the substrate availability was extremely low in our study area. Our results also showed that the Q_{10} values in older stands (PM27 and PM36) were significantly higher than that in younger stands (PM8 and PM17), which is consistent with the findings of previous studies (Y. Ma et al., 2014; Zhao et al., 2016a), but inconsistent with the findings of Tang et al. (2009), who reported that the Q_{10} value decreased with stand age in a chronosequence of deciduous forest. These results emphasize the importance of stand age in controlling Q_{10}. Therefore, as an exponential function of ST without considering stand age impacts, estimated SR can under- or overestimate realistic SR.

4.3. Main environmental factors affecting soil respiration

Several biotic and abiotic factors regulate the variations of SR (Vose and Bolstad, 2007; Peng et al., 2017). Although the correlation analysis showed that SR was significantly correlated with LAI, ST, SOC, TN, C/N and pH, only ST and SOC enter the multiple linear regression equation. This may be attributed to the fact that these factors are closely correlated with each other (Table 4). For example, LAI is positively correlated with SOC and TN ($p < 0.01$), and negatively correlated with pH ($p < 0.01$). In general, ST and SWC were considered as the main factors affecting SR (Zhao et al., 2016a; Powers et al., 2018). However, the results of our study indicate that ST and SOC are the main factors to control SR. This phenomenon might be explained by one or more of the following reasons. First, SWC is a major driver of SR only when soils are extremely dry or extremely wet (Raich and Potter, 1995). Second, the magnitude of SOC content could affect plant growth and stimulate microbial respiration (Uchida et al., 2012). Moreover, heterotrophic respiration is the result of the mineralization of SOC (Knorr et al., 2005). Third, half a century of exploitation of forests and their understories in our study area lead to extremely low SOC (Fig. 2a). With the progress of recovery phase, SOC can slowly increase, and thus stimulate plant growth and increase autotrophic and heterotrophic respiration, which might be more sensitive to SOC than other environmental factors. Therefore, ST and SOC could better explain SR, and it is suggested that the SOC content should be considered when computing SR in the eroded hilly area of southern China.

4.4. Limitations of the current study

Soil respiration rate has obvious spatial and temporal variability (Adachi et al., 2009). The SR measured at sites that are spatially close to each other may vary considerably, especially in the subtropical or tropical forests. Because the observations in this study were only conducted at one site in each age stand, our results might be site-specific in the *P. massoniana* forest. In addition, considering the large fluctuations in environmental conditions in subtropical forests, using the SR data measured only with 3 plots in each stand age for each season might have also affected data quality (Wang et al., 2017) despite the sampling strategy in our study is consistent with the previous studies (Y. Ma et al., 2014; Zhao et al., 2016a). Nevertheless, our results supported one previous study that SR increase with the stand age in *P. massoniana* forest (Xiao et al., 2014). Furthermore, the study site was an area that had experienced serious soil erosion before afforestation. Soil nutrients and vegetation characteristics usually vary with soil erosion and the intensity of human disturbance, which may have a profound influence on the variations of SR. Thus, to further accurately quantify the effects of stand age on SR, it is necessary and important for future studies to conduct long-term and continuous measurement of SR at additional number of replicate stands. Meanwhile, other factors, including human disturbance intensity, fertilization amount, root and microbial biomass, and litter decomposition of each age stand should be assessed in future studies. Nevertheless, our results could be a first step in thoroughly understanding the factors responsible for SR variation.

5. Conclusions

The highest and lowest values of SR were recorded in summer and winter, respectively, regardless of stand age. Seasonal variations in soil respiration may be explained by ST, by using an exponential equation. SR increased with increasing *P. massoniana* stand age. Such effects of stand age on SR were mainly altered by biotic factors (e.g., soil organic carbon, total nitrogen, pH, and LAI), and also abiotic factors (e.g., soil temperature). The Q_{10} values of seasonal SR in the older stands (PM27 and PM36) were significantly higher than that in the younger stands (PM8 and PM17). This study highlights the importance of stand age in regulating soil respiration in *P. massoniana* forests in southern China, and that stand age and seasonal patterns should be considered when predicting carbon budgets under different future climate scenarios.

Conflicts of interest

The authors declare no conflicts of interest.

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